STATOLITH DEVELOPMENT IN THE OMMASTREPHID SQUID *ILLEX ILLECEBROSUS* (LESUEUR, 1821)

CLAUDE C. MORRIS
and
FREDERICK A. ALDRICH
DEPARTMENT OF BIOLOGY
MEMORIAL UNIVERSITY OF NEWFOUNDLAND
ST. JOHN'S, NEWFOUNDLAND

ABSTRACT

Squid of the ommastrephid species *Illex illecebrosus* were collected off Newfoundland, ranging in dorsal mantle length of 13.5–271 mm. Developmental stages of statoliths over this size range are named, described and illustrated. The Juvenile Stage in this series is coincident with the initial development of most adult morphological features.

Statocysts are organs of equilibrium detection found in many motile invertebrates. In cephalopods, they are paired, complex, saccular organs located ventrally within the posterior cephalic cartilage and serve to detect linear and angular accelerations (Figs. 1 and 2.)

Although statolith form varies considerably among teuthoids, several features are common to nearly all. Teuthoid and sepioid statoliths are composed of aragonite (Clarke, 1978), in a thin matrix of protein (Radtke, 1981). Clarke (1978) devised a standard nomenclature for these structures and a system of measurements. Since teuthoid statoliths are apparently species-characteristic and have a greater likelihood of fossilization than other structures, they have potential for identification of fossil species (Clarke and Fitch, 1975). The metrical and nominal descriptive system has been used to identify several new fossil species based on single statoliths (Clarke and Fitch, 1979), recognizing, however, intraspecific variation. Such variation has been demonstrated in *Symplectoteuthis oualaniensis* (Lesson) by Burch (1980), and considerable intraspecific and intra-individual variation has been shown in *Illex illecebrosus* by Morris (1980, 1981). Thus, some doubt may be cast on the validity of descriptions based solely on one statolith from a specimen.

Statolith crystals are in two distinctly different arrangements (Dilly, 1976; Morris, 1980). The first is an irregular arrangement found in the wing, the ventral portion of the dorsal spur, and the medial portion of the rostrum (Fig. 3). These areas appear opaque under a light microscope (Morris, 1980). The second pattern involves nearly parallel orientation of the long axes of the crystals radiating from the nucleus and is found in the dorsal and lateral domes, most of the rostrum and in the central region. These regions are

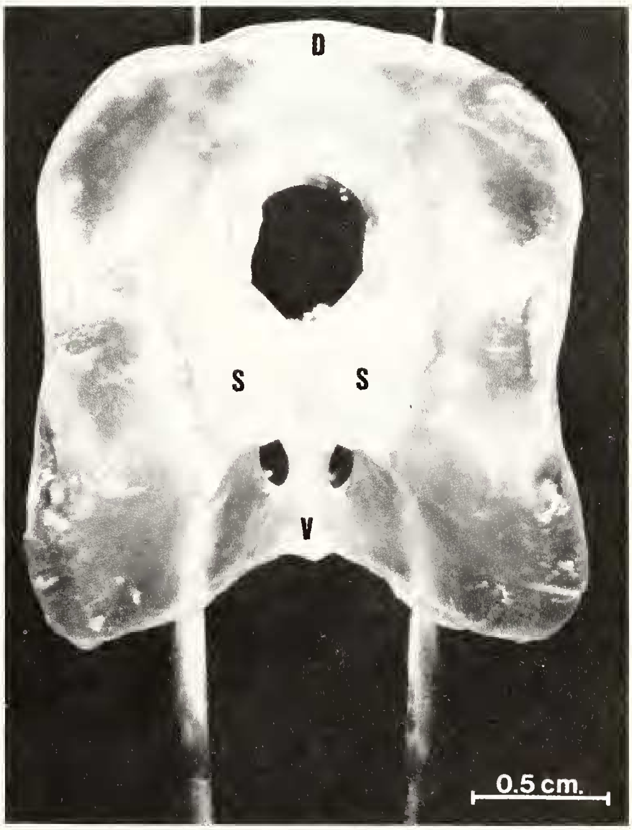

Fig. 1. Photograph showing posterior view of the cephalic cartilage of *Illex illecebrosus* (Lesueur) illustrating the location of the statocysts. (From Morris, 1981). D, dorsal; S, location of statocysts; V, ventral.

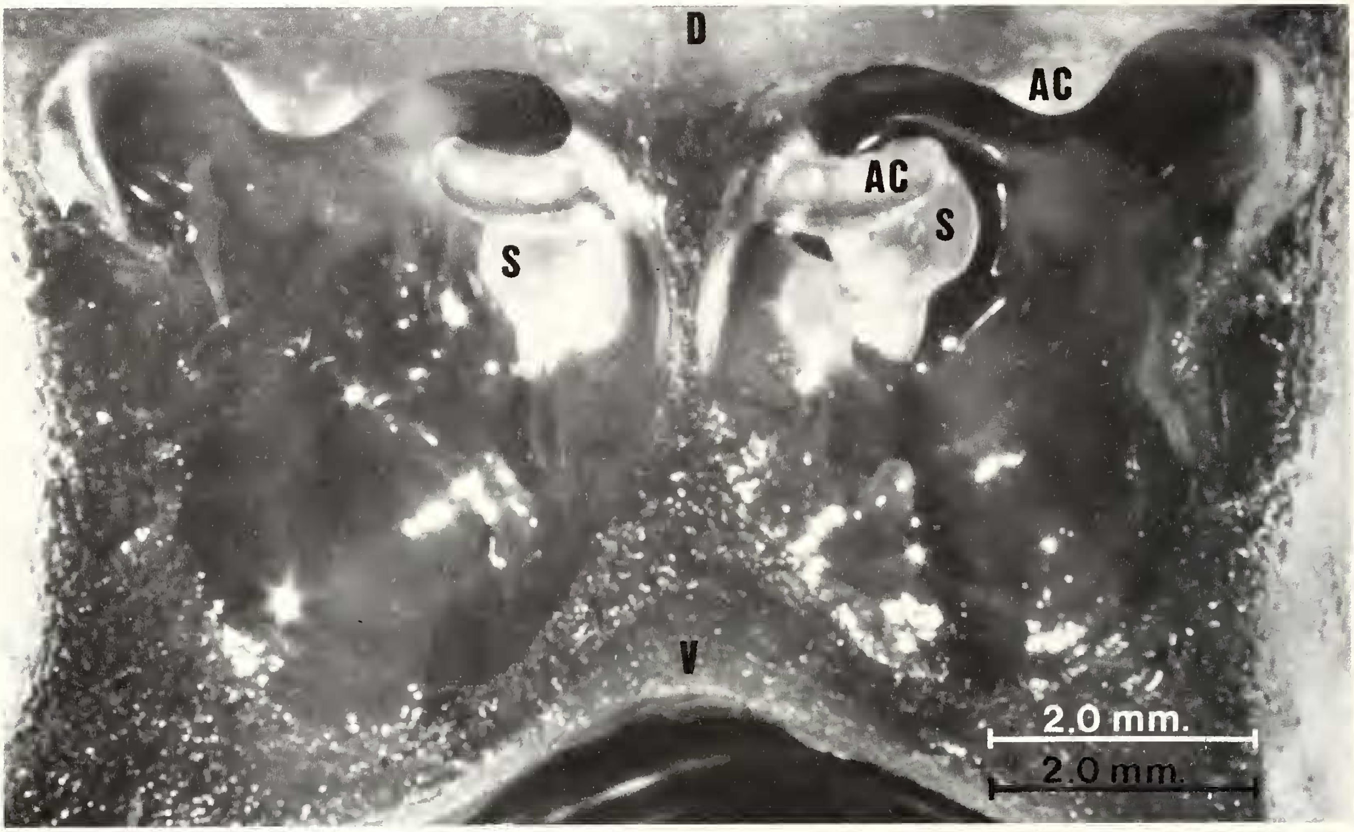

Fig. 2. Photograph of a vertical section through the statocysts of *Illex illecebrosus* (Lesueur) showing the anterior region of the statocysts and the statoliths *in situ*. (From Morris, 1980). AC, anticrista; D, dorsal, ST, statolith; V, ventral.

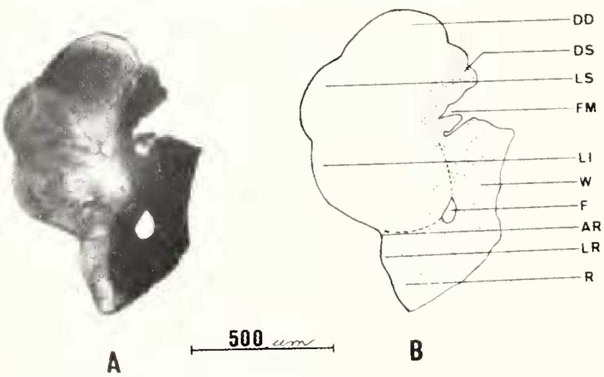

Fig. 3. Posterior aspect of the statolith of *Illex illecebrosus* (Lesueur) showing visible structures referred to in this study. A. Light Micrograph. Notice opaque region composed of irregularly arranged crystals toward medial side of statolith. B. Diagram. Dotted line indicates position of posterior dome indentation. Stippled area indicates region of irregularly arranged crystals. AR, rostral angle; DD, dorsal dome; FM, medial fissure; F, foramen; LI, inferior lobe of lateral dome; LR, lateral lobe of rostrum; LS, superior lobe of rostrum; R, rostrum; DS, dorsal spur; W, wing. (Modified from Morris, 1980: Nomenclature as from Clarke, 1978.)

translucent (Morris, 1980). Growth increments may be visible in these latter areas in unground specimens.

The stages in structural development of a cephalopod statolith are described here for the first time. Lipinski (1980) presented photographs of statoliths of *I. illecebrosus* that show development, but failed to identify developing structures, thus neglecting to trace their developmental anatomy into adulthood.

MATERIALS AND METHODS

Specimens of *I. illecebrosus* were captured on five occasions during 1981 (Table 1 and Fig. 4) and were frozen in sea water until examination.

Statolith removal was performed by placing the squid on its dorsum, lifting the hyponome, and severing the tissues attaching the latter to the head. A vertical incision anterior to the hepatic portion of the digestive gland to the depth of the esophagus exposed the broad posterior cephalic cartilage. Removal of the tissues surrounding this cartilage exposed the two convex cartilaginous protuberances that cover the statocysts. The statoliths were usually visible through the cartilage. A horizontal incision through the posterior cephalic cartilage exposed the statoliths, which were then separated from their maculae and stored in glycerine. Following removal of excess tissue and washing in distilled water, statoliths were photographed in glycerine.

RESULTS

General

In the two earliest samples (February and March, 1981), which contained the smallest specimens (Table 1), the squid exhibited several larval characteristics including a loose saccular mantle, wide proximal aperture of the hyponome, proportionately large eyes relative to the adult, and a posteriorly convex fin. Statoliths were easily removed from even the smallest specimen (13.5 mm DML).

Specimens taken in June were still relatively small, (Table 1), but were similar morphologically to adults captured in October.

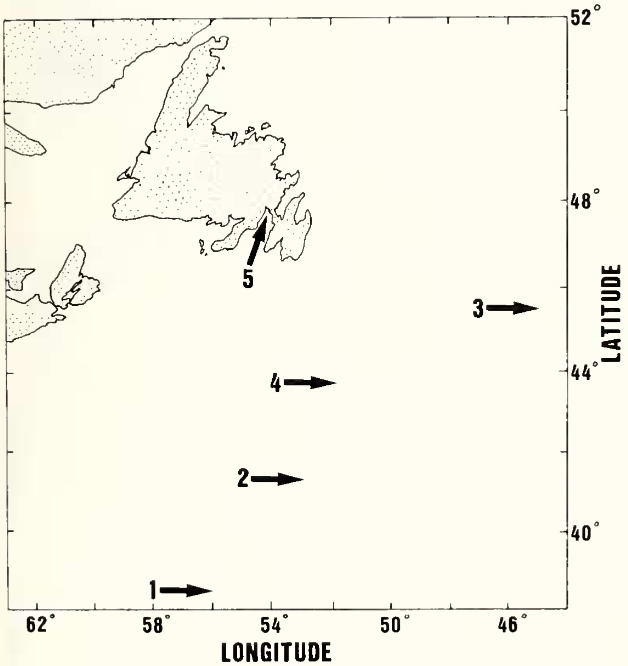

Fig. 4. Map of Northern Gulf Stream region and insular waters of Newfoundland, showing sources of *Illex illecebrosus* (Lesueur). (See Table 1).

Statolith Development

As larger specimens with larger statoliths were taken at progressively later dates, the statolith became increasingly complex and passed through several distinct stages. These stages are described below.

Primordial Stage: The developmental stage that follows nucleus formation has a roughly tear-drop or lachrymiform shape with the tip directed ventrally and flexed slightly anteriorly and laterally (Fig. 5). The Primordial Stage is found in specimens smaller than 14 mm DML. The dorsal region of this structure, the dome anlage, is the precursor of the dorsal dome and superior lateral dome. The medial curvature, after enlarging as the statolith grows, will form the attachment site for the wing. The rostrum anlage is the apex of the lachrymiform structure.

Definitive Stage: The second stage in post-nucleus statolith development, the Definitive Stage, occurs in squid of approximately 30 mm DML (Fig. 6). The dorsal dome, superior lateral dome and inferior lateral dome are forming and easily identifiable. The rostrum is recognizable and is altering its direction of growth, curving toward the midline of the cephalic cartilage *in situ*. The medial aspect of the rostrum bears small irregularly arranged crystals that form the anlage of the wing. Irregular crystals that effectively obscure the underlying increment lines have begun to form in the dorsal region. The dorsal spur begins to form in the dorso-medial region.

Table 1. Dates of capture and sizes of *I. illecebrosus* taken at five sites for statolith analysis, 1981.

Site of capture	Date	No.	Location	Range DML (mm)	Range statolith length (μm)
1.	Feb. 27, 1981	10	38° 24.7′ N 56° 00.0′ W	13.5–29.0	281–442
2.	Mar. 4, 1981	3	41° 14.9′ N 53° 00.0′ W	21–30	366–397
3.	May 25, 1981	5	45° 00.1′ N 45° 30.0′ W	109–118	772–818
4.	June 20, 1981	49	47° 45.1′ N 54° 0.1.2′ W	157–191	851–945
5.	Oct. 15, 1981	48	47° 45.1′ N 54° 01.2′ W	229–271	1033–1139

DML = dorsal mantle length. (See Figure 4)

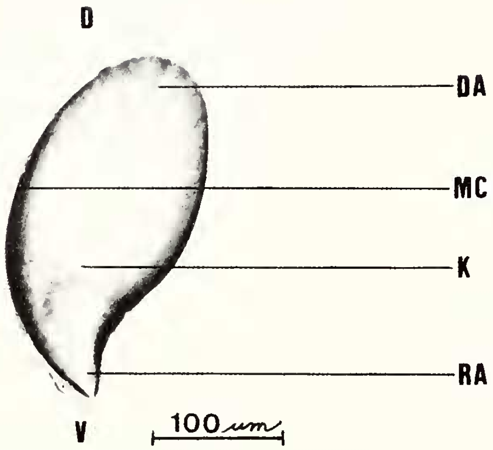

Fig. 5. Primordial Stage in the development of a left statolith of *Illex illecebrosus* (Lesueur) from an unsexed specimen of 13.5 mm dorsal mantle length. (Anterior view). D, dorsal; DA, dome anlage; K, kernel; MC, medial curvature; RA, rostrum anlage; V, ventral.

Pre-Juvenile Stage (Hypothetical): The third stage, the Pre-Juvenile Stage, is not illustrated because of lack of specimens. Several of its characteristics, however, may be inferred. For the sake of continuity we speculate on its appearance and role in the developmental series. The rostrum extends ventrally, and medially. The wing extends medially, then turns anteriorly toward the medial curvature. The dorsal spur is distinct as are the dorsal and lateral domes. Obscuring crystals continue to be laid down on the anterior surface.

Juvenile Stage: In the Juvenile Stage the wing extends upward and connects to the medial curvature, thereby completing a surface that bears a foramen through the statolith (Fig. 7). Further extension of the wing results in the creation of the medial fissure, a discontinuity between the wing ventrally and the dorsal spur dorsally. Obscuring crystals continue to form. This stage is found in specimens of 109 to 118 mm DML.

Adult Stage: The Adult Stage is found in late juveniles and sexually maturing or mature adults (DML over 118 mm). In the adult statolith, the inferior lateral dome may be subdivided so that the entire lateral dome is tripartite (Fig. 8). The foramen gradually becomes filled by the deposition of

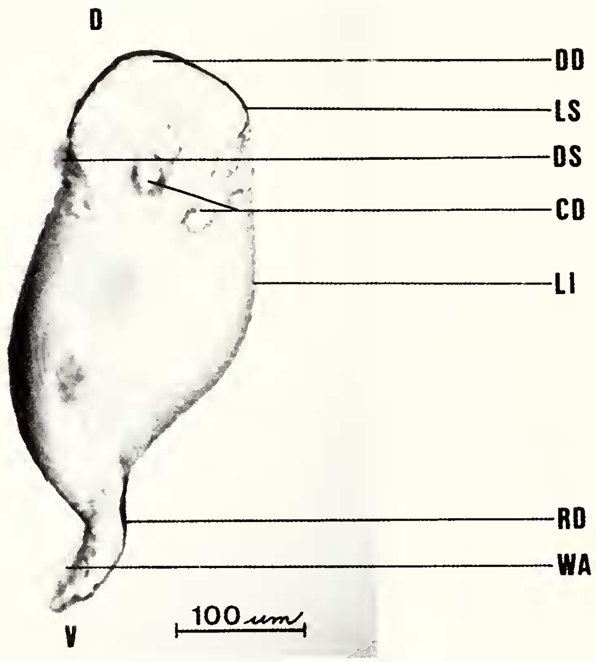

Fig. 6. Definitive Stage in the development of a left statolith of *Illex illecebrosus* (Lesueur) from an unsexed specimen of 29.0 mm dorsal mantle length. (Anterior View). CO, occulting crystals; D, dorsal; DD, dorsal dome; DS, dorsal spur; LI, inferior lateral dome; RO, rostrum; V, ventral; WA, wing anlage.

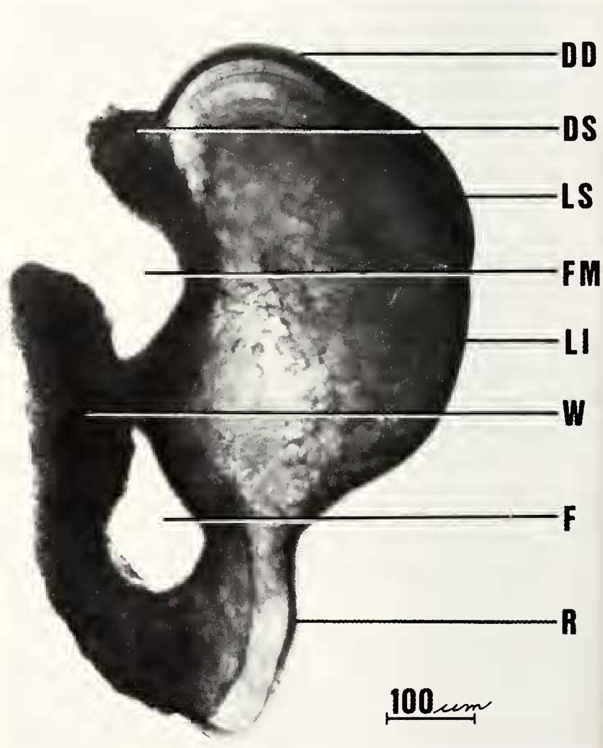

Fig. 7. Juvenile Stage in the development of the statolith of *Illex illecebrosus* (Lesueur) from a female specimen of 109 mm dorsal mantle length. (Anterior view). DD, dorsal dome; DS, dorsal spur; FM, medial fissure; F, foramen; LI, inferior lobe of lateral dome; SS, superior lobe of lateral dome; R, rostrum; W, wing.

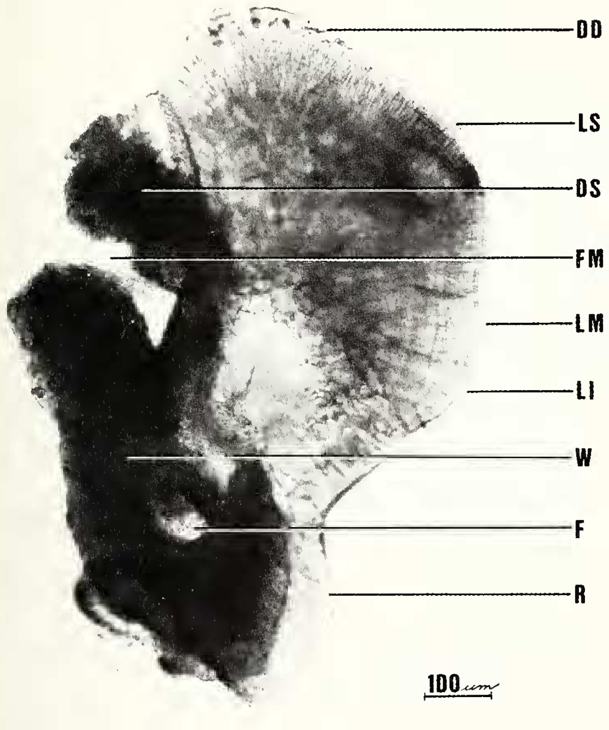

Fig. 8. Adult Stage in the development of the statolith of *Illex illecebrosus* (Lesueur) from a female specimen of 244 mm dorsal mantle length. (Anterior view). DD, dorsal dome; DS, dorsal spur; FM, medial fissure; F, foramen; LI, inferior lobe of lateral dome; LM, medial lobe of lateral dome; LS, superior lobe of lateral dome; R, rostrum; W, wing.

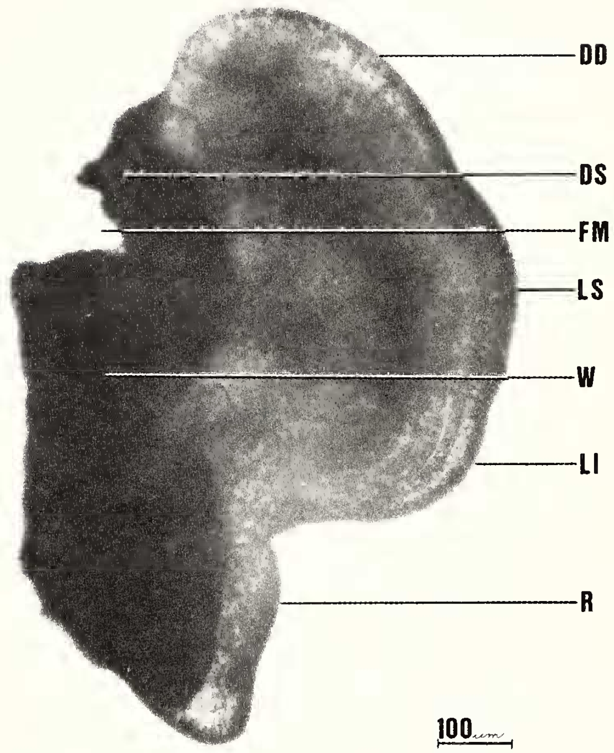

Fig. 9. Advanced Stage in the development of the statolith of *Illex illecebrosus* (Lesueur) from a mature male specimen of DML 230 mm. (Anterior view). DD, dorsal dome; FM, medial fissure; LI, inferior lobe of lateral dome; LS, superior lobe of lateral dome; R, rostrum; DS, dorsal spur; W, wing.

crystals and the medial fissure similarly narrows. Irregular obscuring crystals cover most of the anterior surface of the statolith in this stage, with the exception of the immediate area of the nucleus. It should be noted that these crystals are heavily concentrated in the region of their genesis, indicating their continual production and deposition in that area. The area of their deposition, however, expands with age and time.

Advanced Stage: In the Advanced Stage (Fig. 9), the structure of the statolith is similar to that of the Adult Stage except the foramen and medial fissure are closed, having been filled by crystalline deposits. The lateral dome may or may not be tripartite. Right and left statoliths from the same animal have been seen to vary in having the tripartite condition of the lateral dome in one but not in the other. The Advanced Stage appears in squid of minimum DML of 230 mm.

As the growing statolith passes through these stages, changes in the pattern of increment deposition are visible. These patterns are characteristic of different parts of the translucent portion of the statolith (Morris, 1983).

DISCUSSION

The first part of a teuthoid statolith to be formed and subsequently recognized during development is the kernel. The kernel, not to be confused with the nucleus which includes the kernel (Morris, 1983), is a small spheroidal area lying near the wing of the statolith in the adult animal. It is visible in statoliths from very young specimens (Fig. 5) and in ground statoliths from adult specimens. Growth increments in the kernel are absent or indistinct.

The kernel is analogous to the kernel of fish otoliths in representing the formation or growth of the statolith prior to the deposition of clearly recognizable increments. Thus, the statolith exists in the form of a very small kernel before the deposition of the first increments. The nucleus of fish otoliths consists of the kernel plus the first opaque increment (Pannella, 1980). Such a prominent increment can be found around the kernel of statoliths of squid (Figs. 5 and 6), thus distinguishing the kernel from the adjacent extranuclear area.

A basic change in overall shape throughout the developmental sequence is apparent. Early, the basic configuration is lachrymiform (Primordial Stage, Fig. 5) and this shape can be traced by following incremental darkenings around the nucleus (Fig. 6). Soon the lachrymiform shape is altered as the statolith enters the Definitive Stage (Fig. 6) at which time *I. illecebrosus* has attained a dorsal mantle length in excess of 14 mm. The larval stage of the ommastrephid family is classically considered to end with the separation of the proboscis to form the tentacles, thus ending the rhynchoteuthoid stage (Chun, 1915). This occurs at DML of 8.5–9.5 mm (Roper & Lu, 1978, Vecchione, 1978). The statolith development, however, indicates that the larval stage is still present at DML of 14 mm, which suggests that larval biology and morphology extend beyond the rhynchoteuthion.

The anlagen, or precursors, of specific statolith structures so evident in the Adult Stage first arise during the Definitive Stage. The single exception to this is the rostrum anlage, which is first evident in the Primordial Stage. Indeed, the rostrum has assumed a configuration clearly similar to that of the adult as early as the Definitive Stage.

During the Pre-Juvenile stage, the anlagen are developed to such an extent that the statolith is characterized by all the adult structures in their proper adult positions and in approximate adult proportions.

Although there are some morphological changes in statoliths between Juvenile and Adult Stages, most changes are associated with increase in size. As expected, squid with juvenile statoliths have a body morphology which is essentially that of the adult (except for size and sexual organ development). The level of development of body morphology and associated maneuvering ability are apparently reflected in the degree of complexity and developmental stage of the statoliths.

A clear demarcation between Juvenile and Adult statolith forms is not obvious, but the ventral portion of the medial fissure is widely open in the Juvenile Stage and closes in the Adult, and the foramen of the Juvenile shows no crystalline deposits.

The Advanced Stage is very uncommon, having been found in less than 1% of the more than 400 pairs of statoliths of *I. illecebrosus* examined. Although specimens with the foramina filled are often found, an accompanying closure of the medial fissure is atypical, particularly to the extent illustrated in Figure 9. This form, i.e. the Advanced Stage, may be within the range of normal variation expected in the adult configuration, but at present we have no basis for an explanation of this phenomenon. We suggest that it represents the final configuration of the statolith typical of the Ommastrephid after it has left the insular waters of Newfoundland and begins its supposed southerly migration into its oceanic habitat.

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